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Multilevel feeding ecology – an introduction

Monika Trienens¹, Jan Bruin² & Leo W. Beukeboom^{1*}

¹Groningen Institute of Evolutionary Life Sciences (GELIFES), University of Groningen, Nijenborgh 7, 9747 AG Groningen, The Netherlands, and ²Institute for Biodiversity and Ecosystem Dynamics (IBED), Evolutionary and Population Biology, University of Amsterdam, Science Park 904, 1098 XH Amsterdam, The Netherlands

Undoubtedly, one of the most essential demands for all living organisms is the acquisition of nourishment in sufficient quantity and quality to grow and reproduce. The first challenge is to find food sources. Volatile organic compounds (VOC) – for example, emitted by plants – are among the cues that may help herbivores to locate suitable host plants (e.g., Dancewicz et al., 2016; Jacobsson et al., 2016; Koschier et al., 2017; but see also Finch & Collier, 2012; Carvalho et al., 2017). Volatile organic compounds profiles emitted by insect-infested plants may in turn be utilized as infochemicals by parasitoids or predators to find their hosts and prey (e.g., Steidle & van Loon, 2003; Peñafior et al., 2017; Thanikkul et al., 2017). A further step in detecting nutritious food is to discriminate between favourable and less beneficial food sources, based on small-scale differences caused by, for instance, differential accessibility and digestibility of tissues, infection by endophytic fungi, or variation in toxic substances among host plants and plant parts (e.g., Harvey & Malcicka, 2016; Rizvi & Raman, 2016; Zhao et al., 2017). This special journal issue on multilevel feeding ecology of insects addresses aspects of host location, performance, and plant defence responses, that are of relevance for improving our understanding of the complex interactions within ecological communities and that will support advances in biological control.

The preference–performance hypothesis predicts that females will choose to oviposit on plants that maximize offspring development (‘mother knows best’) (e.g., Friberg & Wiklund, 2016; Smith et al., 2016). However, empirical tests do not always support this hypothesis. Altesor & González Ritzel (2018) demonstrated that females of the monophagous sawfly *Tequus schrottkyi* (Konow) (Hymenoptera: Pergidae) clearly preferred to oviposit on their natural host plant, the wild potato *Solanum commersonii* Dunal (Solanaceae), over the cultivated potato, *Solanum tuberosum* L. They also found that *T. schrottkyi* performed

better when raised on the preferred plant, and concluded further that the better performance was not due to higher nutrient quality, but that differences in concentration and composition of toxic steroidal glycoalkaloids between the *Solanum* species may directly or indirectly influence the performance.

A further study testing the preference and performance of an herbivore was conducted by Cao et al. (2018). Their study organism was the green peach aphid, *Myzus persicae* (Sulzer) (Hemiptera: Aphididae), that was fed on detached *Brassica oleracea* L. (Brassicaceae) leaves of various ages. Amino acid and glucosinolate concentrations differed between leaf ages, and although aphid performance, inferred by weight, was intermediate on young leaves, the young leaves showed the highest attraction to aphids – not directly in line with the preference–performance hypothesis.

Multiple studies have shown that plants are no passive victims to herbivory but are able to mount considerable defence responses to diminish or even eradicate herbivores, and thus to minimize the damage that herbivores inflict, by producing toxic secondary metabolites or by recruiting natural enemies. These responses can be triggered by elicitors – or *herbivore-associated molecular patterns* (HAMPs) – which involve, for example, salivary proteins introduced into the plant during feeding. However, the herbivorous insects themselves and also their (endo)symbionts may interfere with these defence responses by means of effectors that potentially interrupt the defence–response cascade of the plant.

Bayendi Loudit et al. (2018) analysed the diversity of endosymbionts in *Aphis craccivora* Koch (Hemiptera: Aphididae, Aphidini) clones, and the protein composition of soluble and solid saliva that are both injected by the aphids into host-plant tissues. Fifteen percent of the proteins detected in aphid saliva was of bacterial origin. In lieu of synthesizing toxic secondary products themselves, some plant species have acquired symbionts that can produce these substances, which may repel herbivores. Shymanovich & Faeth (2018) investigated the effect of such symbionts in a system of pooid grass, *Achnatherum robustum* Vasey (Poaceae), and fungal symbionts of the genus

*Correspondence: Leo Beukeboom, Groningen Institute of Evolutionary Life Sciences (GELIFES), University of Groningen, Nijenborgh 7, 9747 AG Groningen, The Netherlands.
E-mail: l.w.beukeboom@rug.nl

Epichloë (Hypocreales). The effect of two fungal symbiont species, *Epichloë funkii* and *Epichloë* sp. nov., were tested on survival, development, fitness, and behaviour of the insect herbivore *Spodoptera frugiperda* Smith (Lepidoptera: Noctuidae), the fall armyworm. Thus, both conflicting parties, that is, the herbivorous insect and the plant, may recruit symbionts to help them in their battle.

Parasitoids and predators are often employed for biological control of pest species as an alternative to synthetic pesticides. To deploy the recruitment of parasitoids to reduce herbivory in crop plants, a deep understanding of their attraction to plant-derived volatile cues is needed. Mao et al. (2018) explored the attractiveness of 17 selected volatiles from three major structural groups of rice plants to the rice planthopper egg parasitoid *Anagrus nilaparvatae* Pang et Wang (Hymenoptera: Mymaridae). Rice planthoppers (Hemiptera: Delphacidae) are a serious crop pest in Asia. The results of Mao et al. (2018) may help to develop the means to beacon *A. nilaparvatae* towards pest-infested areas, and thus to reduce crop loss due to herbivory while also reducing the use of toxic insecticides.

Predatory ladybird species (Coccinellidae) are frequently used in greenhouses as biocontrol agents against aphids. The predation rate and performance of *Adalia bipunctata* L., *Hippodamia variegata* Goeze, and *Scymnus interruptus* Goeze (all Coleoptera: Coccinellidae) fed on *M. persicae* infesting sweet pepper was tested by Beltrà et al. (2018). The authors discuss their results with respect to sustainable use and application purpose, may it be curative or preventive, and conclude that the most voracious species may not always be the best choice.

Adults of parasitoids in search of hosts for oviposition depend on energy uptake in form of carbohydrate-rich food sources. To improve the performance of parasitoids in biological control it has been recommended to plant nectar-producing flowering plants near the crop fields. Munir et al. (2018) investigated the effect of four carbohydrate sources, three of them Brassicaceae species, on the parasitoid *Diadegma insulare* Cresson (Hymenoptera: Ichneumonidae) and its host *Plutella xylostella* L. (Lepidoptera: Plutellidae). The carbohydrate sources increased the longevity of both the herbivore and its parasitoid. Hence, to identify a specific nectar source that favours the parasitoid more than the herbivore, for example, due to morphological accessibility, will be crucial for biocontrol purposes.

The present issue is completed by a technical note of Visschers et al. (2018), presenting a high-throughput screening method for quantifying herbivore damage caused by cell-sucking insects, such as thrips. For biting/chewing herbivores the standard practice is to measure the

removed leaf area; however, sucking insects cause a different damage pattern, and thus a different way to determine the degree of damage is required. The automated protocol employs freely available software, which makes it widely applicable.

This special journal issue reflects that ecological communities form complex interacting networks, where insect–plant interactions are further influenced by other herbivore and host-plant species, by mutualistic and antagonistic microorganisms, as well as by abiotic constraints, such as climate change (Giron et al., 2018). Understanding mechanisms and functions in multilevel feeding interactions will advance the increasing efforts to substitute the extensive use of chemical pest control agents, which harbour tremendous environmental drawbacks, by more environmental friendly means for sustainable agriculture and lasting human food production.

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